

Theoretical analyses of testing efficiency in long-term breeding of poplar

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Abstract: The major goal for long-term poplar breeding can be formulated as maximizing annual progress in Group Merit Gain at a given annual budget (GMG/Y^*). To evaluate different breeding scenarios, a deterministic simulator BREEDING CYCLE ANALYZER covering the most important aspects (gain, cost, time, technique, and gene diversity) of a full breeding cycle was used. The breeding strategies considered was based on pairwise crossing of the selected breeding population and balanced within family selection for the next breeding population. A main scenario and a number of alternative scenarios within these constraints were evaluated using estimates of the best available inputs for poplars. In focus was a comparison between three different testing scenarios for selecting the parents mated to create future breeding generations, thus selecting based on phenotype, clone test or progeny test. For the main scenario, the highest GMG/Y and the optimal selection age for clone, phenotype and progeny strategies were 0.7480 %, 0.6989 % and 0.4675 %; 7, 6, and 11 years respectively. Clone test was best except when heritability was high, plant price was high or total budget was low; phenotype strategy was the second except for the case of extremely low narrow-sense heritability, for which the progeny strategy was a little more efficient than phenotype strategy. GMG/Y was markedly affected by narrow-sense heritability, additive variance at mature age, rotation age, plant-dependent cost, total budget and the time needed to produce the test plants, while diversity loss and recombination cost had rather weak effect on GMG/Y . Short rotation age and cheap testing cost favoured all three testing strategies. Comparably short rotation age, low plant-dependent cost and high total budget seem to promote early selection for progeny strategy.

Keywords: Poplar; Group merit gain; Testing efficiency; Breeding strategy; Clonal testing; Progeny testing

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Introduction

Poplars are widely cultivated in many countries of the temperate and subtropical regions because of their easy vegetative propagation, fast growth, wide adaptation, extensive interspecific cross ability, and manifold utilization. Selections from cultivated or natural forests have been done and mated, and hundreds cultivars have been selected from interspecific hybridization for commercial plantations, which characterized the history of poplar breeding. This can be seen as the initiation of a breeding program. At some stage of a breeding program has to process to be long term. This means that it is composed of repeated cycles of selection (based on some form of test) and recombination (mating of the selected parents). However, Long-term breeding strategies of poplars has been suggested but only to a very limited extent (Bisoffi and Gullberg, 1996), still more efforts are focused on short-term rather than long-term breeding due to the consideration of economical goals; or, possibly, lacking of suitable tools to combine genetic diversity, genetic gain, genetic parameters, cost, time and other factors into long-term poplar breeding strategy.

Maintaining genetic variation and creating new material with reasonable high breeding value for commercial use are two ma-

jor objectives for long-term forest tree breeding. Generally three ways of testing (by phenotypes, clones or progeny) can be used to select member of next breeding population. It is necessary to compare the relative efficiencies of three testing methods. To evaluate relative efficiency, the breeding value, gene diversity, time, cost and technique should be considered simultaneously (Lindgren and Mullin 1997; Rosvall *et al.* 1998; Wei and Lindgren 2002); Methods combining these considerations for long term breeding, which will be used here, has been developed by Danusevicius and Lindgren (2001, 2002) and resulted in the EXCEL program BREEDING CYCLER.

Group Merit Gain (GMG) is a weighted average of breeding value and genetic diversity, therefore, the major goal for long-term breeding is to maximize annual progress in Group Merit Gain at a given annual budget (GMG/Y^*). Although some studies have investigated the efficiencies of different testing strategies (Burdon 1986; Shelbourne and Jordaan 1991; Foster 1992; Mullin and Park 1992; Wei 1995; Meuwissen and Soneson 1998), none of them had consideration with gain, diversity, cost and time simultaneously. The aim of this paper is to approach an optimizing breeding strategy theoretically in long-term poplar breeding considering cost, time, genetic parameters and annual budget simultaneously.

Methods

Poplar breeding plan and basic assumptions

Here we take the case of black poplar such as *populus nigra* L., *populus deltoids* Marsh, *populus euramericana*, which is adapted from Italian breeding program for poplars (Bisoffi and Gullberg 1996), to make the long-term poplar breeding plan.

Maintaining a meta-population made up from a number of un-

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related breeding populations of 50 members each.

Double-pair mating among 50 members within each breeding population.

Balanced within family selection of one individual per full-sib family as a parent for next breeding cycle.

Basic assumptions:

The infinitesimal genetic model was assumed.

Breeding value of selected founders was set to zero.

No G × E interaction.

No C-effects nor epistatic variance was considered.

To get a scale the average breeding value of the parents at the start of the cycle was arbitrarily set to zero (or rather 100%).

Genetic gain prediction and simulation software

Group Merit Gain per year (*GMG/Y*) is the objective criterion to be maximised, and Group Merit Gain (*GMG*) is obtained by the following Equation:

$$GMG = G - c\Theta \quad (1)$$

where, *G* is the estimated additive genetic gain at rotation age, *c* is a weighting factor, and Θ the diversity loss per breeding cycle in term of increment in group coancestry, which, assuming that each parent contributes two offspring to be used as the parents in the next breeding cycle, was estimated as:

$$\Theta = 0.25 / n \quad (2)$$

where, *n* is the number of the individuals selected (Wei and Lindgren 2002).

The genetic gain at rotation age was calculated by the following equation (Lindgren and Werner 1989):

Phenotype strategy:

$$G = \frac{\sigma_{Am} r_{j-m} i \sigma_A}{\sqrt{\sigma_A^2 + \sigma_D^2 + \sigma_E^2}} \quad (3)$$

Clone strategy:

$$G = \frac{\sigma_{Am} r_{j-m} i \sigma_A}{\sqrt{\sigma_A^2 + \sigma_D^2 + \frac{\sigma_E^2}{n}}} \quad (4)$$

Progeny strategy:

$$G = \frac{\sigma_{Am} r_{j-m} 0.5 \sigma_A}{\sqrt{0.25 \sigma_A^2 + \frac{0.75 \sigma_A^2 + \sigma_D^2 + \sigma_E^2}{n}}} \quad (5)$$

where: *G* is the additive genetic gain in percentage, σ_A^2 the additive variance, σ_D^2 the dominance variance, σ_E^2 the environmental variance, *n* the number of plants per family, σ_{Am} the standard deviation in breeding value of the selected individuals for a target trait at rotation age and is given as percentage of the average breeding value of the unimproved individuals for this trait (one standard deviation is equal to 10%), *i* the selection intensity estimated by the method of BURROWS (1975), and r_{j-m} the juvenile-mature (J-M) genetic correlation estimated according to the Equation by Lambeth (1980):

if $0 < Q < 0.1$, then $r_{j-m} = Q \times 3.108$

if $0.1 \leq Q \leq 0.9$, then $r_{j-m} = 1.02 + 0.308 \times \text{Log}(Q)$ (6)

if $0.9 < Q \leq 1$, then $r_{j-m} = 0.988 + (Q - 0.9) \times 0.012/0.1$

where *Q* is the ratio of selection age to rotation age.

The time of one breeding cycle consists of the following four components:

$$T_{\text{CYCLE}} = T_{\text{RECOMB}} + T_{\text{BEFORE}} + T_{\text{TEST}} + T_{\text{AFTER}} \quad (7)$$

where, T_{RECOMB} is the recombination time, T_{BEFORE} the time needed to produce plants for the selection test (from seeding in nursery to planting in the field test), T_{TEST} the time needed for testing and selection, and T_{AFTER} the time from selection of the new parents to harvest of their seeds for the next breeding cycle.

The total cost per breeding cycle was expressed as:

$$C_{\text{PER CYCLE}} = C_{\text{RECOMB}} + C_{\text{INIT}} + n(C_G + m C_P) \quad (8)$$

where C_{RECOMB} is the cost for recombination among the founders, C_{INIT} the cost for initiation of the test, C_G the cost per genotype, C_P the cost per test plant, *n* is number of genotypes (Ortets for clonal test of female parents for progeny test), and *m* the number of plants (Number of ramets per clone in clonal test or number of seedlings per family in progeny test).

A deterministic simulator "BREEDING CYCLE ANALYZER" based on the genetic gain prediction and Equations above was used (Available on the WEB at www.genfys.slu.se/staff/dag1). Long term breeding can be described as cyclic population improvement over repeated cycles of mating, testing and selection. Breeding cyclers is a tool for evaluation over a cycle, which also can be used for optimization. It follows the breeding operations for a full cycle. Multi-generation breeding is multiple repeats of such breeding cycles. Tree breeders may identify a best breeding strategy considering genetic gain, gene diversity, cost, time and testing strategy by experiment with the deterministic simulator. The simulations were done according to the main and the alternative scenarios (Table 1). While testing an alternative value of a parameter, all the other parameters should be kept at the values for the main scenario. The variable parameters to search for maximum *GMG/Y* at a given cost were age of selection, family size, number of ramets for clonal testing and number of half-sib progeny for progeny testing.

Values of parameters for simulations

Genetic parameters for the main scenario were chosen to represent growth traits of poplar according to most results (Li *et al.* 1994; Stettler *et al.* 1996). Additive standard deviation at mature age (σ_{Am}) was set to 10 % for the main scenario, and to 5% and 20% for the alternative scenarios, respectively. The initial additive variance within family was set constant to 1, and dominance and environmental variances were expressed as ratios of the additive variance. The dominance variance was set to make up 25% of the additive variance in the breeding population for the main scenario, and 0% and 100% for the alternative scenario. Narrow-sense heritability in the breeding population was set to 0.1 for the main scenario and 0.05 and 0.5 for the alternative scenarios (Table 1).

For the main scenario, the weighting factor for loss of diversity (c) was set to 100 to make it equally compatible with genetic gain, and for the alternative scenarios, the weighting factor was set to result in a loss of diversity of 0.1% and 1%, respectively (Table 1). For the main scenario, the timing for certain operations

was chosen to be in agreement with the practical experience with poplars, and for the alternative scenarios, proportion of main scenario value (Table 1). The cost value was chosen based on the case of China (Table 1).

Table 1. Parameters used by simulation.

Items	Parameters	Main scenario	Alternative scenarios
Genetic parameters	Additive variance (A^2)	1	
	Dominance variance (D^2), % of A^2	50	0; 100
	Narrow-sense heritability (h^2)	0.2	0.01; 0.5
	Additive standard deviation at mature age (A_m), %	10	5; 20
	Diversity loss per cycle, %	0.5	0.1; 1
Cost per breeding population member (\$)	Recombination cost (C_{RECOMB})	10	1; 20
	Cost per genotype (C_g)	0.1 (Cl), 1 (Pr)	1; 10 (Cl), 0.1; 10 (Pr)
	Cost per plant (C_p)	1	0.1; 10
	Cost per year and parent (constraint)	10	5; 20
Time (year)	Time before establishment of the selection test (T_{BEFORE})	2 (Ph)	1; 3 (Ph)
		3 (Cl)	1; 6 (Cl)
		6 (Pr)	3; 12 (Pr)
	Rotation age	15	8; 30

Note: BP means breeding population. (Ph) phenotype strategy, (Cl) clone strategy, (Pr) progeny strategy.

Results

General results

Under the most likely parameter values, the testing efficiencies (GMG/Y) of clone, phenotype and progeny strategies were 0.7480%, 0.6989 % and 0.4675%, respectively (Table 2). Clone test was the best strategy except for cases of high heritability, high plant price or low total budget. Phenotype strategy was the second except for the case of extremely low narrow-sense heritability, for which the progeny strategy was lightly more efficient than phenotype strategy (Table 2).

Genetic parameters and breeding efficiency

According to Equation (6), the J-M genetic correlations based on main scenario for clone, phenotype and progeny strategies were 0.8974, 0.9182 and 0.9785, respectively. Reduction in dominance variance increased GMG/Y for all three strategies, but more for the clone strategy and less to progeny strategy. Even if dominance variance would be 100% of the additive variance, GMG/Y obtained from the clone strategy is still 6.75% and higher than GMG/Y from the phenotypic strategy and 33.67% higher than that from progeny strategy (Table 2, Fig. 1a).

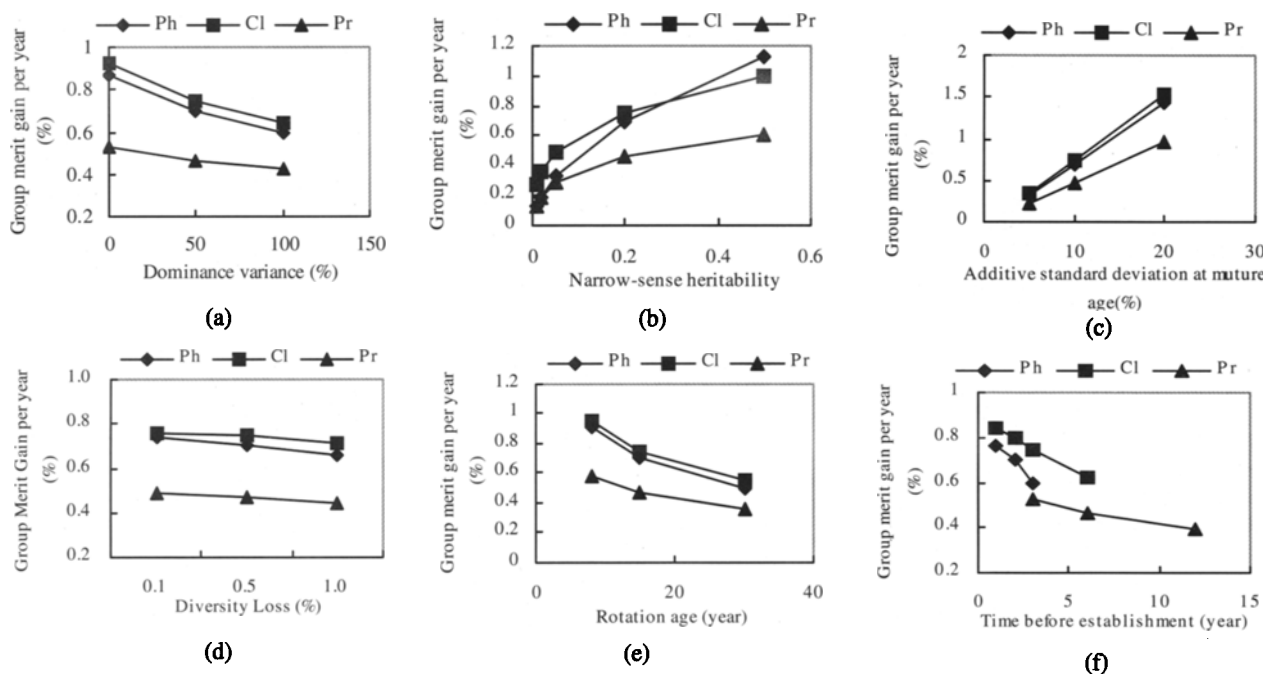


Fig. 1 Group merit gain per year (GMG/Y) as a function of testing strategy and values of genetic parameters (a, b, c, d), rotation age (e) and time before establishment of selection test (f). Note: Ph---Phenotypic strategy, Cl---clone strategy, Pr---progeny strategy.

Narrow-sense heritability has an effect on *GMG/Y* for all the strategies. Increase of h^2 may change the ranking of three strategies. Phenotypic strategy became superior over the clone strategy when heritability exceeded 0.5, and at the heritability lower than 0.01, progeny strategy was superior over clone strategy (Fig. 1b).

As expected, a higher value of genetic variance at mature age (σ_{Am}) markedly improved *GMG/Y* (Fig. 1c) for all strategies. However, a higher loss of gene diversity had a minor effect on *GMG/Y* for all the breeding strategies (Fig. 1d). With increasing importance of gene diversity, *GMG/Y* from the phenotype strategy decreased somewhat faster than *GMG/Y* from the other breeding strategies (Fig. 1d).

Optimum number of test plants

The optimum number of test plants was 29 ortets per family

with 4 ramets each for clone strategy, and the optimum family size was 12 individuals with 15 seedlings each for progeny strategy, and 99 individual for phenotype strategy (Table 2).

For the clone strategy, *GMG/Y* increased with increasing number of ortets and decreasing number of ramets per ortet in the selection test. A similar tendency was also observed for the progeny strategy (Table 2). Increase in σ_{Am} had a little effect on optimum number of test plants for all breeding strategies. Short rotation age markedly reduced optimum number of test plants for phenotype strategy and had little effect for the other strategies (Table 2). As expected, cost per test plant and total budget had marked effects on the number of tested plants for all the testing strategies (Table 2).

Table 2. Efficiency of different testing strategies under different circumstances evaluated as Group Merit Gain per year (*GMG/Y* in %). Optimum selection age and number of test plants calculated for each set or parameter values. The best testing strategy under the circumstances is indicated by bold.

Parameters	Value	Phenotype strategy			Clone strategy				Progeny strategy			
		<i>GMG/Y</i>	Age to select	Family size	<i>GMG/Y</i>	Age to select	Ortet no.	Ramet no. per ortet	<i>GMG/Y</i>	Age to select	Female parent no.	Progeny no. per parent
D^2 , % of A^2	0	0.8668	6	98	0.9251	7	29	4	0.5286	10	14	12
	50*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	100	0.5994	6	100	0.6428	7	30	4	0.4264	10	10	17
h^2	0.01	0.1234	8	119	0.2729	11	7	23	0.1340	13	6	34
	0.02	0.1911	7	111	0.3596	10	9	16	0.1903	12	6	33
	0.05	0.327	6	104	0.4942	8	13	10	0.2856	12	7	28
	0.2*	0.6989	6	99	0.748	7	29	4	0.4675	11	12	15
	0.5	1.1319	6	97	1.001	7	55	2	0.6085	10	18	9
σ_{Am} , %	5	0.327	6	104	0.3552	8	31	4	0.2214	11	12	15
	10*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	20	1.4442	6	96	1.5348	7	29	4	0.9616	10	11	15
Diversity loss, %	0.1	0.7363	6	95	0.7601	5	31	3	0.4873	11	12	15
	0.5*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	1.0	0.654	6	104	0.7103	8	31	4	0.4428	11	12	15
Rotation age, (year)	8	0.9085	5	85	0.9524	5	33	3	0.5735	7	11	13
	15*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	30	0.4978	8	124	0.5489	10	36	4	0.357	12	12	16
Time before establishment of selection test, (year)	1	0.7583	5	84	0.8379	8	27	4				
	2 ^{Ph}	0.6989	6	99	0.7958	6	33	3				
	3 ^{Cl}	0.5943	3	84	0.748	7	29	4	0.5245	9	10	13
	6 ^{Pr}				0.6231	12	40	5	0.4675	11	12	15
	12								0.3927	13	14	18
Recombination cost, \$	1	0.7083	6	106	0.7604	7	33	4	0.4750	10	12	15
	10*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	20	0.6874	6	91	0.734	8	28	4	0.4597	11	11	15
Cost per test genotype, \$	0.1 ^{Cl}				0.748	7	29	4	0.4766	10	13	14
	1.0 ^{Pr}				0.7049	9	24	5	0.4675	11	12	15
	10				0.5469	9	9	6	0.4037	12	7	19
Cost per test plant, \$	0.1	0.9868	5	1944	1.086	6	139	7	0.7886	8	32	40
	1.0*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	10	0.4192	8	12	0.3953	11	8	2	0.1914	11	6	3
Total budget, \$	5	0.6095	6	47	0.5834	4	20	2	0.3548	15	9	11
	10*	0.6989	6	99	0.7480	7	29	4	0.4675	11	12	15
	20	0.7763	6	202	0.8642	7	47	5	0.5771	9	17	20

Note: The symbol in the superscript of the parameter values indicates the main scenario value for: (*) all breeding strategies, (Ph) phenotype strategy, (Cl) clone strategy, (Pr) progeny strategy. Selection age was counted from establishment of the selection test.

Optimum age for selection

For the main scenario, the optimum selection ages for phenotype, clone and progeny strategies were 6, 7 and 11, respectively. As regards the effect of the parameters within each testing alternative, optimum selection age was mainly influenced by narrow-sense heritability, rotation age, and time component (Table 2). Increase of narrow-sense heritability greatly reduced the optimum selection age for the clone and progeny strategies, but had relatively minor effect on optimum selection age for the phenotype strategy. Reduction of rotation age led to a shorter selection age for all the breeding strategies (Table 2).

Discussion

What is important in long-term poplar breeding?

The current schemes of most poplar breeding programs, in which hybridizations were made among superior individuals from breeding population, followed by commercial varieties selection which was generated from progeny population based on the results of clone testing, pay little attention not only to genetic testing for members of breeding population but also to the view of long-term breeding (Bisoffi and Gullberg 1996). Since the genetic potential of poplars for interspecific breeding and clonal selection has been well demonstrated across the world, the prevailing view among poplar breeders is to adopt schemes that focus on gains to be made in one or two generations, although advanced-generation breeding had been advocated by some breeders (Bisoffi and Gullberg 1996).

In long-term poplar breeding, maintaining genetic diversity and creating commercial varieties are two equal objectives. To select member of next breeding cycle, the candidate needs to be tested, otherwise, the virtue of varieties generated for next

breeding population can not be ensured. On the commercial or economical viewpoint, increase in gain in terms of breeding value is the overall goal indeed, but it often leads to diversity loss due to the application of high selection intensity. Therefore, it needs to be balanced between gain and diversity in a poplar breeding program, in other words, the long-term poplar breeding should be one in which long-term (Diversity) and short-term (Gain) were integrated successfully.

Normally in clone selection of poplar, progeny strategy is rarely used to test poplar clones owing to its superiority of vegetative propagation. However, since the progeny testing is the only way to report the additive variances (breeding value) of individuals especially in the breeding population, it should be taken into consideration when the members of breeding population need to be tested.

Which is the best strategy for genetic testing of breeding population in poplar?

The superiority of clone selection to other strategies had been well proven not only theoretically but also practically, and here a similar result was obtained based on the analyses of *GMG/Y* under balanced within family selection (Table 1, Figs. 1, 2). However, an interesting finding is that *GMG/Y* obtainable from clone strategy remained high under most of the parameter values simulated, including high cost for cloning and high dominance variance (Figs. 2b and 1a). The negative effect of dominance variance seemed to be minor if compared with the advantage in prediction of breeding value by clonal testing. As clone testing is done routinely for short term breeding in poplars, it seems to be good news that no extra complicated progeny-testing activity seems to be needed for long-term breeding.

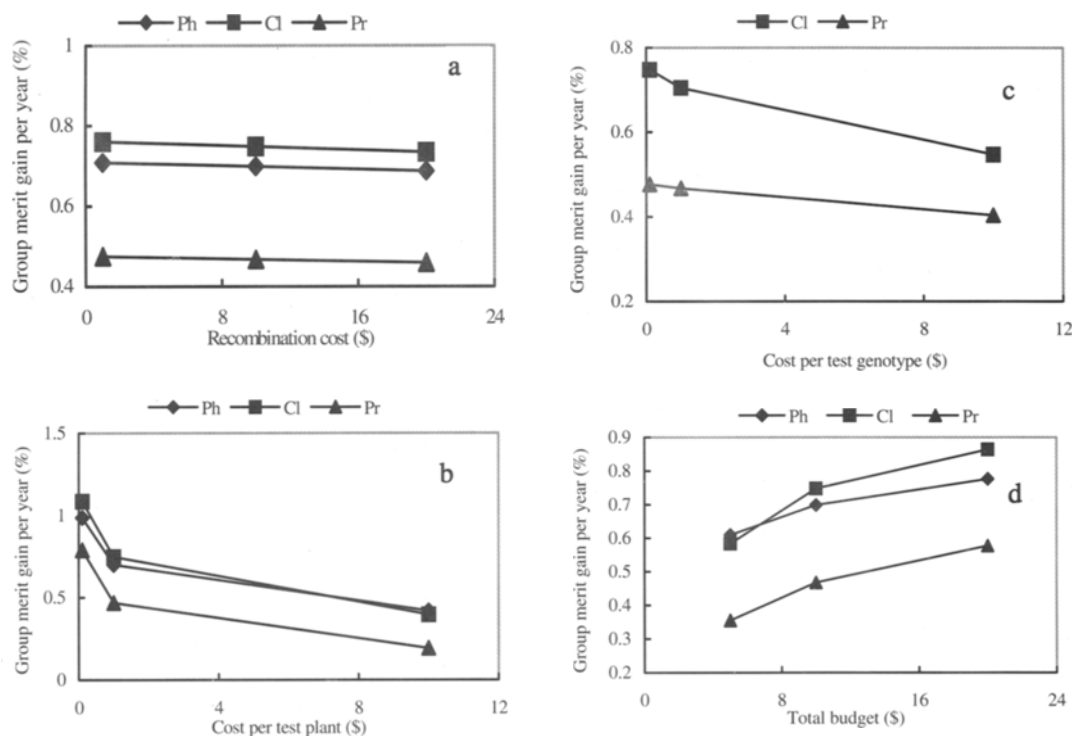


Fig. 2 Ranking between the breeding strategies in *GMG/Y* at the main and alternative values for cost components

Note: Ph---Phenotypic strategy, Cl---clone strategy, Pr-- progeny strategy.

Undoubtedly, progeny testing is able to predict the breeding value better than phenotype testing, but still we obtained a reverse result that progeny strategy resulted in a lower *GMG/Y* compared with phenotype strategy under most circumstances (Fig. 1b).

Phenotype strategy can perform its superiority to other strategies when narrow-sense heritability is high. High heritability means a high correlation existed between phenotype and genotype. Therefore, it is not necessary to use a large number of test plants. Phenotype strategy is a better choice in contrast to the clone and progeny strategies when narrow-heritability is higher than 0.35 (Fig. 1b), but such a high heritability is not so common.

How do genetic parameters affect the breeding efficiency of poplar?

It is certain that genetic parameters could affect breeding efficiency, but what is the extent of effects for different breeding strategies is not certain. For all three breeding strategies studied, narrow-sense heritability, mature additive variance had stronger effect on *GMG/Y*, while dominance variance, gene diversity loss had comparably weaker effect on *GMG/Y*.

The genetic parameters used for simulation of main scenario were based on the growth traits of black poplar (section *Aigeiros*). They are related to the traits studied, for example, the broad-sense heritability of *Populus deltoides* for growth, rooting ability and disease resistance is 0.21-0.5, 0.33-0.58 and 0.66-0.88, respectively (Bisoffi and Gullberg 1996). Therefore, clone strategy is favourable for traits like growth and rooting ability, while for disease resistance, the phenotype strategy may be more efficient.

Besides genetic parameters, other factors had also great effect on breeding efficiency. Rotation age, time before establishment of the selection test, cost per genotype, cost per test plant, and annual budget had stronger effect on *GMG/Y* (Figs. 1e, 1f, 2b, 2c, and 2d), whereas recombination cost had little effect on *GMG/Y* (Fig. 2a).

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